

CYTOTAXONOMIC STUDIES IN THE TRIBE QUILLAJEAE (ROSACEAE)¹

PETER GOLDBLATT²

ABSTRACT

The following chromosome numbers were found in previously uncounted genera of Quillajae: $n = 17$ in *Lindleya* and *Kageneckia*, and $n = 15$ in *Vauquelinia*. An earlier count of $n = 27$ in *Lyonothamnus* is confirmed, but *Quillaja*, previously reported as $n = 17$ is shown to have $n = 14$ in both species currently recognized. This variety of chromosome numbers supports the widely held contention that the tribe is unnatural. *Lindleya* is regarded here as a member of the Maloideae, where $x = 17$ is basic, and *Vauquelinia* is suggested as best placed in this subfamily. The genus *Exochorda*, known to have $n = 8$, appears to accord with Prunoideae ($x = 8$), particularly with *Oemleria*, while *Lyonothamnus* seems best left in Spiraeoideae ($x = 9$). The peculiarities of the remaining genera, *Kageneckia* and *Quillaja*, suggest that they be placed in a separate subfamily.

Traditionally the Rosaceae have been treated as comprising six subfamilies, or as in more recent treatments four, with the Neurodoideae and Chrysobalanoideae recognized as distinct families. The remaining subfamilies, Spiraeoideae, Prunoideae, Maloideae and Rosoideae, are by and large natural groupings and, as might be expected from so ancient and comparatively primitive dicot group, relatively distinct from one another. This classical treatment of the family is supported by chromosomal data. The basic chromosome number in the family appears almost certainly $x = 9$ (Raven, 1975) and this base number is found in the Spiraeoideae (with several notable exceptions) usually regarded as the least specialized of the four subfamilies with its partly to completely free carpels and dry, usually follicular fruits. In the subfamily Prunoideae the base number is $x = 8$, in the Maloideae, $x = 17$ (clearly a palaeotetraploid group), and while a base number of $x = 7$ predominates in the Rosoideae, $x = 9$ and $x = 8$ also occur in several lines.

The Spiraeoideae appear to be the least homogeneous of the rosaceous subfamilies, the discordant elements being a number of genera usually placed in the tribe Quillajae, which have in common dry, dehiscent fruits with winged seeds. In its broadest sense (Hutchinson, 1964) the tribe comprises the following genera: *Quillaja*, *Kageneckia*, *Vauquelinia*, *Lindleya*, *Exochorda*, and *Lyonothamnus*. The last-mentioned is included only by Hutchinson and differs in having two to three carpels in contrast to five in the other genera, and, in spite of statements to the contrary, its seeds are not winged. Various authors since Spach

¹ I would like to thank Peter H. Raven, Director of the Missouri Botanical Garden, for his encouragement in this project and assistance in obtaining material for study, and W. G. D'Arcy, also of the Missouri Botanical Garden for his helpful comments. Thanks are also extended to the following for their cooperation and help in obtaining the seed or cytological material used in this study: Jerzy Rzedowski, Escuela de Ciencias Biológicas, Mexico City, Mexico; Marshall C. Johnston, University of Texas, Austin, Texas; Charles T. Mason, University of Arizona, Tucson, Arizona; Bruce Bartholomew, Berkeley Botanical Garden, Berkeley, California; Barbara Lilley, University of California, Stanford, California; Ramon Ferreyra, Herbario San Marcos, Lima, Peru.

² B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

(1834: 429), who excluded the Quillajaeae from the Spiraeoideae, have implied or stated that the tribe is not a natural alliance. Schulze-Mentz (1964), for example, admits only *Quillaja*, *Kageneckia* and *Vauquelinia*, while placing *Exochorda* and *Lindleya* in the Exochordeae and *Lyonothamnus* in the Sorbarieae. Certainly, differences between some genera of the Quillajaeae seem greater than between other tribes and even subfamilies of the Rosaceae. This is reflected in what little has been known of the cytology of the group with reported chromosome numbers in three genera ranging from $n = 27$ ($x = 9?$) in *Lyonothamnus*, $n = 7$ in *Quillaja*, and $n = 8$ in *Exochorda* (Table 1), the latter genus already associated with the Prunoideae because of its cytology (Raven, 1975). Thus cytological data amplifies the likelihood that the alliance is unnatural.

The present study was undertaken in the hope that a more comprehensive knowledge of the cytology of the tribe will lead to a better understanding of the affinities of the genera placed in the Quillajaeae and of the overall evolution in the Rosaceae.

CYTOLOGY

Chromosome counts were made either from anther squashes or root tips, and counts (Table 1) are accordingly reported as gametic or somatic. Fixed buds for meiotic study were either collected from wild plants, in the case of *Lindleya* and *Vauquelinia corymbosa*, or from cultivated material from a known wild source, *Kageneckia oblonga*, *K. angustifolia*, and *Quillaja saponaria*. Mitotic studies were made from root tips collected from germinating seeds grown at the Missouri Botanical Garden. Seeds of *Kageneckia lanceolata* and *Vauquelinia angustifolia* were collected from wild plants, while seed of *Quillaja brasiliensis* and *V. californica* were obtained from plants in cultivation.

Buds were fixed in 1:3 acetic:ethanol and stained in propionic carmine. Root tips were pretreated either in hydroxyquinoline or 0.1% colchicine for 4 hours, fixed, macerated in 10% HCL for 4 minutes and squashed in lactopropionic orcein.

The results presented in Table 1 are briefly summarized as follows. All species of *Vauquelinia* studied have a chromosome number of $n = 15$, the three species of *Kageneckia* have $n = 17$, and the monotypic *Lindleya* has $n = 17$. The report for two species of *Quillaja*, both $n = 14$, is in sharp contrast to the previous report for this genus, $2n = 34$ (Bowden, 1945). Bowden's report was for *Q. brasiliensis*, also studied here, and in the light of the present records of $n = 14$ in two species of *Quillaja*, Bowden's count can only be viewed with misgiving. It was probably based on material of some species of Maloideae, and no voucher seems to exist.

The previous report on $n = 27$ for *Lyonothamnus* (Raven et al., 1965) is confirmed here, for the same subspecies, subsp. *asplenifolius*. The tentative count of $2n = 48$ (Stebbins & Major, 1965) in *L. floribundus* thus was only approximate, as suggested by Raven et al. (1965). The only genus of the tribe not examined in the present work, *Exochorda*, is known to have $n = 8$ (Table 1).

DISCUSSION

With each of the four subfamilies of the Rosaceae (excepting the tribe Quillajaeae) having a different and characteristic base number, the variation in

TABLE 1. Chromosome numbers in the tribe Quillajeae sensu lato. Whenever known, complete collection data and voucher information is presented. Counts determined during this investigation in **bold face**.

Species	Chromosome No.		Collection Data and/ or Author Citation
	Gametic	Somatic	
<i>Exochorda</i>			
<i>giraldii</i> Hesse	8		(Sax, 1931: cult. Arnold Arboretum, Cambridge, Mass.; collection data not known, no voucher kept).
<i>tianschanica</i> Gontsch.	8		(Federov, 1969).
<i>Kageneckia</i>			
<i>angustifolia</i> D. Don	17		Cult. Carnegie Inst. of Washington, Stanford, Calif.; seed ex Chile, Prov. Santiago, Yeso Valley, <i>Mooney SA80</i> (DS).
<i>lanceolata</i> R. & P.	17		Cult. Missouri Botanical Garden; seed ex Peru, Dept. Ayacucho, San Juan de Lucanas, <i>Ketcham 80</i> (MO).
<i>oblonga</i> R. & P.		34	Cult. Carnegie Inst. of Washington, Stanford, Calif.; seed ex Chile, Quebrada de la Plata, <i>Mooney SA73</i> (DS).
<i>Lindleya</i>			
<i>mespiloides</i> H.B.K.	17		Mexico, Querétaro, near Maconi, <i>Rzedowski 31605</i> (ENCB).
<i>Lyonothamnus</i>			
<i>floribundus</i> Gray		48	(Stebbins & Major, 1965: cult. Berkeley, Calif.; ex California, Santa Cruz Island).
<i>floribundus</i> subsp. <i>asplenifolius</i> (Greene) Raven	27		(Raven et al., 1965: cult. Rancho Santa Ana Botanic Garden, Claremont, Calif.; ex California, Santa Cruz Island, <i>Wolf 4129</i> (RSA) progeny.
	27		Collection data same as above.
<i>Quillaja</i>			
<i>brasiliensis</i> (St. Hil.) Mart.	17		(Bowden, 1945: seed ex Botanical Garden, Montevideo, Uruguay, no voucher kept).
		28	Ex hort. Station de Botanique et de Pathologie Vegetale, Antibes, France.
<i>saponaria</i> Mol.	14^a		Cult. Univ. of California Botanical Garden, Berkeley, Calif.; seed ex Chile, Prov. Santiago, Maipú Valley, <i>West 6010</i> (UC).
<i>Vauquelinia</i>			
cf. <i>angustifolia</i> Rydb.		30	Mexico, Chihuahua, near Coyama <i>Wendt et al. 9841</i> (MO).
		30	Mexico, Chihuahua, Sierra de Chrysaderos, <i>Johnston 8907</i> (TEX).
<i>californica</i> Sarg.		30	Ex hort. C. T. Mason, Arizona, <i>Mason s.n.</i> (MO).
<i>corymbosa</i> Correa	15		Mexico, Hidalgo, Atotonilco el Grande, <i>Rzedowski 31515</i> (ENCB).

^a Count made by G. Davidse, Botany Department, Missouri Botanical Garden.

chromosome number within the Quillajae appears all the more startling. If the Quillajae is regarded in its broadest sense (Hutchinson, 1964), this single tribe is as heterogeneous chromosomally as the whole family Rosaceae. However, it is clear that the tribe cannot be considered a natural alliance and some genera at least can be reclassified with some degree of confidence in the light of the cytological evidence.

EXOCHORDA

The concurrence of the base number of *Exochorda*, $x = 8$, with that of the Prunoideae suggests this as a more suitable taxonomic position, though at first glance the 5-carpellate ovary and dry, capsular fruit of *Exochorda* seem misplaced in the Prunoideae. However, comparison with the isolated prunoid genus, *Oemleria* (*Osmaronia*), unusual in having a 5-carpellate drupaceous fruit, brings to light a number of similarities. Both *Exochorda* and *Oemleria* have obsolete stipules and a similar 5-carpellate ovary with two epitropic ovules, the latter condition a characteristic though not unique prunoid condition.

Exochorda, the only member of the Quillajae which has a base number at the diploid level, does in fact seem particularly misplaced in this tribe and its transfer to the Prunoideae appears warranted. Sterling (1969) has pointed out that *Oemleria* is anatomically rather isolated from other members of the Prunoideae and proposed segregating it as a distinct tribe, Osmaronieae. The inclusion of *Exochorda* in this tribe, within the Prunoideae, may be the most satisfactory way to reflect the natural relationships of the genus.

LINDLEYA

Since *Lindleya* has the same base number, $x = 17$, that is characteristic of the Maloideae, its association with the Quillajae and the Spiraeoideae appears highly questionable. Of fundamental importance is the validity of the traditional distinction between the two subfamilies. Maximowicz (1879) considers the pome, with its fleshy receptacle, the only difference between the Maloideae and Spiraeoideae. With certain Quillajae excepted, the free carpels of the Spiraeoideae provide a second important difference between the subfamilies. Since the spiraeoid base number, $x = 9$, invariably is linked with free carpels, and the maloid base number, $x = 17$, is associated with a fleshy and syncarpous fruit, *Lindleya* may well be better placed in this latter group, even though it has a dry fruit. Sterling (1966) has commented that the carpels of *Lindleya* are fused in the manner very characteristic of the Maloideae. Other authors also have associated *Lindleya* with this subfamily on anatomical grounds, notably Bonne (fide Sterling, 1966), who strongly links *Lindleya* with *Mespilus*. There is also phytochemical evidence linking *Lindleya* with the Maloideae since the phenolic, isochlorogenic acid (Challice, 1973) found in many Maloideae, occurs in *Lindleya* and in no other Spiraeoideae. Challice (1974) has, however, found that the chemotaxonomically significant flavone C-glycosides found in many, but not all, Maloideae are absent in *Lindleya*.

There is obviously a strong argument to be made for considering genera such

as *Lindleya* intermediate between the Spiraeoidea and Maloideae, and it certainly has morphological and chemotaxonomic features of both. However, the very characteristic base number, $n = 17$, makes it appear that the affinities of *Lindleya* lie with the Maloideae rather than with the Spiraeoideae. Transfer of *Lindleya* to the Maloideae is perhaps the best taxonomic solution to the problem.

KAGENECKIA

With cytology of all three species in the genus known, it is evident that *Kageneckia*, with $n = 17$, has the same base number as that occurring in the Maloideae. It is, however, difficult to envisage a close relationship between *Kageneckia* and this subfamily. Its carpels are free (confirmed anatomically by Sterling, 1966), and contain many predominantly pleurotropic ovules, whereas the ancestral condition for the Maloideae is probably biovulate (Sterling, 1969). There is, however, some resemblance between the carpels of *Kageneckia* and those of the multiovulate maloid genera such as *Cydonia*. The possibility that this is a reflection of phylogenetic relationship is perhaps enhanced by the concurrence of basic chromosome number, but nevertheless seems unlikely, unless the Maloideae are regarded as polyphyletic, having originated from ancestral lines with dry, biovulate, syncarpous and multiovulate, apocarpous gynoecia. Chemotaxonomic evidence, although negative, (Challice, 1974) makes it even more unlikely that *Kageneckia* is related to this group of Maloideae as it lacks the characteristic isochlorogenic acid and flavone C-glycosides found in many maloid genera.

Kageneckia exhibits considerably greater resemblance to the other South American member of the alliance, *Quillaja*, which the present study indicates has $n = 14$. The two have similar carpels (although in *Quillaja* they are partly united) and remarkably similar fruits and seeds. The morphological similarities between these two genera are such that it seems most likely that they are indeed related, notwithstanding the impressive differences in basic chromosome number and in chemistry, with the significant flavone C-glycosides occurring in *Quillaja* but not in *Kageneckia* (Challice, 1974).

QUILLAJA

Both species of *Quillaja* have $n = 14$, despite Bowden's (1945) earlier record to the contrary. The base number $n = 14$ for the genus contrasts strikingly with $n = 17$ for *Kageneckia*, probably its closest ally, and it is equally discordant either with the Spiraeoideae or Maloideae (a concurrence with the most common base number, $x = 7$, in the Rosoideae must be regarded as coincidental, and of no phylogenetic significance).

The partly united carpels of *Quillaja* appear to differ only to a small degree from those of *Kageneckia* and in my opinion these two genera are relatively primitive in the Rosaceae. The peculiar and very primitive flavonoid chemistry of *Q. saponaria*, described by Bate-Smith (1965), also supports this contention. Leucodelphinidin occurs only in this species and in the rest of the Rosaceae only in one species of *Potentilla*.

The South American distribution of *Quillaja* and *Kageneckia* contrasts with a predominant Northern Hemisphere distribution for the Rosaceae, and the presence of an ancestral stock in South America suggests the possibility that the family, now poorly represented in the southern continents, may have once been more developed there. The family may have had its origin in West Gondwanaland, i.e., South America and Africa, away from the region of its present concentration, or it may have arrived in South America very early, perhaps via Africa (Raven & Axelrod, 1974), though *Kageneckia* and *Quillaja* have no close relatives in that continent today.

Quillaja and *Kageneckia* appear to represent an ancient line, perhaps derived from spiraeoid ancestors collaterally with the Maloideae. With its partly united carpels *Quillaja* would appear more specialized than *Kageneckia*, and this perhaps accords with its lower base number, $x = 14$, if $x = 9$ is indeed primitive for the family.

VAUQUELINIA

The affinities of this Mexican and southwestern United States genus of small trees are particularly problematic since its base number, $x = 15$, is unique in the Rosaceae. It has 5 biovulate carpels united in the maloid manner, and the apotropic ovules also accord with those of the Maloideae. Except for its different chromosome number, *Vauquelinia* would accord almost as well as *Lindleya* with the Maloideae morphologically, though there appear to be no chemotaxonomic links between *Vauquelinia* and the Maloideae.

Vauquelinia is sometimes associated with the California Island endemic *Lyonothamnus*, which has $n = 27$ (and probably $x = 9$), a relationship strongly supported by Banwar (1966). Several disparities must however be noted. First, *Lyonothamnus*, with unusual opposite leaves, has two (or three) free carpels each with several epitropic ovules. Second, the seeds differ; those of *Lyonothamnus* lack the wing found in *Vauquelinia* and other Quillajeae. In fact, *Lyonothamnus* accords well with the Spiraeoideae, particularly in critical floral and fruit characteristics. With its presumed base number the same as that of the Spiraeoideae, *Lyonothamnus* appears best treated as a rather isolated genus in this subfamily and not closely associated with *Vauquelinia*. On present evidence it appears best to regard *Vauquelinia* as most closely related to *Lindleya* and thus falls marginally into the Maloideae. It is however sufficiently discordant here, both chromosomally and morphologically, that it is only with hesitation that I suggest it be assigned to the Maloideae. Further investigation of this curious genus may bring to light more information on the relationships.

CONCLUSION

The cytology of the tribe Quillajeae lends considerable support to the belief that this is an unnatural alliance and that most of its constituent genera are misplaced in the Spiraeoideae, a group otherwise characterized by free carpels and dry fruits and a basic chromosome number of $x = 9$. The following changes in taxonomy of the Rosaceae are proposed: *Exochorda* is assigned to the Prunoideae-

Osmaronieae; *Lindleya* and *Vauquelinia* to the Maloideae; and *Lyonothamnus* to the Spiraeoideae, perhaps in a separate tribe. In the light of these changes, the subfamilies of the Rosaceae all require limited redefinition. The Maloideae, with $x = 17$ (and 15 in *Vauquelinia*), have carpels united to one another and to the receptacle and have usually fleshy pomes, but also capsular fruits. The latter condition is perhaps ancestral. In the Prunoideae, with $x = 8$, the drupaceous fruit is characteristic but not definitive, the carpels are free to united but not to the receptacle, and the fruit is a capsule or drupe. In Spiraeoideae, with $x = 9$, the carpels are free and the fruit is a follicle (or achene).

This leaves *Quillaja* and *Kageneckia* unaccounted for and they are perhaps best regarded as constituting a distinct subfamily, developed collaterally with the Maloideae from an ancestral spiraeoidlike stock, and retaining many ancestral characteristics. Cytological and chemotaxonomic data suggest that these two genera are not particularly closely allied, yet morphological similarities dictate their inclusion in the same subfamily or tribe.

LITERATURE CITED

- BANWAR, S. C. 1966. Morphological and anatomical studies on the genus *Lyonothamnus*. Ph.D. dissertation. University of California, Berkeley.
- BATE-SMITH, E. C. 1962. The phenolic constituents of plants and their taxonomic significance I. Dicotyledons. *J. Linn. Soc. Bot.* 58: 95-173.
- . 1965. Investigation of the chemistry and taxonomy of sub-tribe Quillajeae of the Rosaceae using comparisons of fresh and herbarium material. *Phytochemistry* 4: 535-539.
- BOWDEN, W. 1945. A list of chromosome numbers in the higher plants. II. Menispermaceae to Verbenaceae. *Amer. J. Bot.* 32: 191-201.
- CHALLICE, J. S. 1973. Phenolic compounds of the subfamily Pomoideae: a chemotaxonomic survey. *Phytochemistry* 12: 1095-1101.
- . 1974. Rosaceae chemotaxonomy and the origins of the Pomoideae. *Bot. J. Linn. Soc.* 69: 239-259.
- FEDEROV, A. A. (editor). 1969. Chromosome Numbers of Flowering Plants. Izdatel'stvo Nauka, Leningrad.
- HUTCHINSON, J. 1964. The Genera of Flowering Plants. Vol. 1. Clarendon Press, Oxford.
- MAXIMOWICZ, C. J. 1879. Adnotationes de Spiraeaceis. *Trudy Imp. S.-Peterburgsk. Bot. Sada* 6: 105-261.
- RAVEN, P. H. 1975. The bases of Angiosperm phylogeny: Cytology. *Ann. Missouri Bot. Gard.* 62: 724-764.
- & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- , D. W. KYHOS & A. J. HILL. 1965. Chromosome numbers of spermatophytes, mostly Californian. *Aliso* 6: 105-113.
- SAX, K. 1931. The origin and relationships of the Pomoideae. *J. Arnold Arbor.* 12: 3-22.
- SCHULTZE-MENTZ, E. K. 1964. Rosales. In H. Melchior (editor), *A. Engler's Syllabus der Pflanzenfamilien*. Ed. 12. Vol. 2: 193-243.
- SPACH, M. E. 1834. *Histoire Naturelle des Végétaux*. Vol. 1. Librairie Encyclopédique de Roret, Paris.
- STEBBINS, G. L. & J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35: 1-35.
- STERLING, C. 1966. Comparative morphology of the carpel in the Rosaceae. IX. Spiraeoideae: Quillajeae. Sorbarieae. *Amer. J. Bot.* 53: 951-960.
- . 1969. Comparative morphology of the carpel in the Rosaceae. X. Evaluation and summary. *Oesterr. Bot. Z.* 116: 46-54.